EYES OF DEEP-SEA CRUSTACEANS

II. Sergestidae

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Introduction

In the first of this series of papers which dealt with the eyes of the Acanthephyridae (Welsh and Chace, 1937) it was shown that *Hymenodora glacialis*, a species of deep-sea prawn which normally lives at a level below the photic zone, has quite degenerate eyes, while related species which normally inhabit the photic zone have well-developed and obviously functional eyes. It was also shown that among the acanthephyrids of the photic zone those possessing photophores have larger eyes in proportion to body size than those which lack the means to produce light of their own. Since such correlations between the structural development of the eye, light intensity and the ability to produce light are of considerable interest from the standpoint of adaptation, the present study of the eyes of the Sergestidae was undertaken with these points in mind.

Much of the literature dealing with the eyes of deep-sea crustaceans was cited in the paper already referred to and since collecting methods were also discussed in this paper and one by Welsh, Chace and Nunnemacher (1937), it will be unnecessary to discuss these matters further.

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Characteristics and Distribution of the Sergestidae

The prawns which make up the family Sergestidae form a well-defined, aberrant group of the most primitive tribe of the Natantia, the Penaeidea. Since the species dealt with in this paper belong, in the main, to the genus *Sergestes* it is not necessary to dwell on the four remaining genera of the group.

[1] Contribution No. 176.

All of the species of *Sergestes* are slender-bodied animals with long, slender appendages (Fig. 1) and an integument that is never as firm as in most of the acanthephyrids. Despite their fragile appearance, most of the species retain their form and appendages fully as well as most other pelagic decapods when subjected to the usual handling. The last two pairs of thoracic legs are flattened and shorter than the other three pairs and fringed with long hairs. These, in conjunction with the long, well-developed pleopods suggest that the sergestids are among the fastest swimming of the pelagic Crustacea. Further indication that such is the case is provided by the fact that very few adult specimens and practically none of the mature individuals of the larger species were captured until the advent of the motor-driven vessel which was able to tow nets at a fairly rapid rate of speed. In collections now made with modern ships and apparatus, however, sergestids are very frequently encountered, and a number of the North Atlantic species are apparently reasonably abundant in the midwater area; possibly the commonest species in any one region is the luminous species, *Sergestes lucens* Hansen, from off Japan, of which 10 million pounds are said to be taken annually by commercial fisheries.

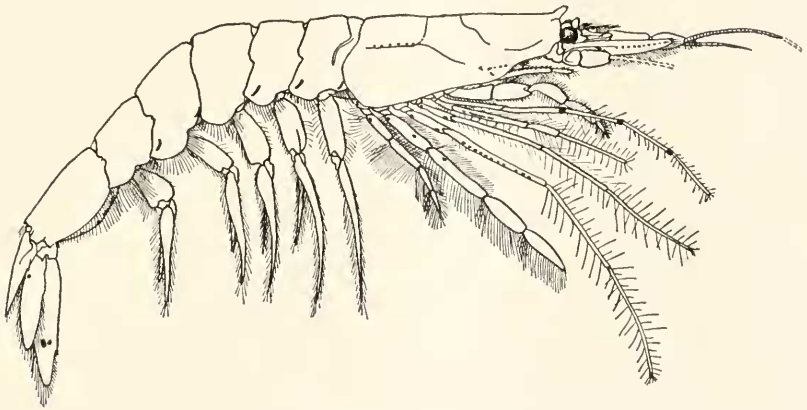


FIG. 1. *Sergestes grandis* Sund, female, showing certain of the features which characterize sergestids. Photophores, which are present only in certain species, are indicated by solid black spots.

The lack of adult individuals and the extremely long and complicated larval history of these animals were the chief obstacles in the path of the correct determination of species by the early carcinologists. Innumerable species have been described, a great many on larval forms, and it was not until the last few years that any idea of the number of valid species could be learned. It is estimated that there are between

thirty and thirty-five species of *Sergestes,* and even now several comparisons, particularly between Atlantic and Pacific specimens, are necessary before the exact number of known forms can be ascertained.

Although they inhabit the general "black fish-red prawn" area, only two of the sixteen species known from the North Atlantic are distinctly red in color. The others range from a deep rose pink and a pattern of red spots to almost perfectly transparent forms in which the internal organs may be clearly seen.

In 1903 photophores or luminescent organs were observed for the first time in any species of the genus and since then they have been described in four other species. Recently organs which are probably photophores have been detected in three other Atlantic species. It is very probable that further study of fresh material will show that about a dozen species possess these structures. So far as we are aware no instance of the discharge of a "luminous cloud" such as observed in several other bathypelagic forms has as yet been recorded for these forms.

The species are most abundant in tropical and sub-tropical areas, being most numerous in the Atlantic between the Tropic of Capricorn and 30° North Latitude. Although fourteen of the sixteen species known from the North Atlantic area were taken by "Atlantis" at Stations 2666 (39° N., 70° W.) and 2667 (35° N., 69° 36′ W.), only three species have been taken by any expeditions north of 47° N. Lat. The horizontal distribution of the species of *Sergestes* is similar to that of other bathypelagic decapods; several species have been taken at numerous localities throughout the world, while others have a restricted distribution with closely related species inhabiting corresponding areas in other oceans.

Comparatively little is known of the vertical distribution of these animals. This is far from surprising when one realizes that previous expeditions have for the most part used open nets, which are perhaps more likely to catch animals when the net is being raised to the surface than at any other time. Also, most expeditions have covered a wide area and an attempt has been made in the reports to combine into one table the depth records for each species from these widely scattered localities. When one considers that probably no condition save pressure is everywhere constant at a given depth; when one realizes that light intensity, temperature, oxygen content and the chemical composition of the water all vary markedly at different localities at a stated depth, it is no less than amazing that certain species are apparently found at so nearly similar depths in all parts of the area in which they are encountered. Until exhaustive collections are made with closing nets at single

stations and the results examined separately we will continue to be quite ignorant of the optimum conditions preferred by the various species. Table I gives a very rough idea of the depths at which the various

TABLE I

Depths in meters at which adult specimens of *Sergestes* have been taken with closing nets by "*Atlantis*." [2]

	0	200	400	600	800	1000	1200	1400	1600	1800	2000	2050
Sergestes												
mollis[3]	..	..	..	X	X	X	..	..	X	X	X	X
sargassi	..	..	X	..	X	..	..	..	X			
pectinatus	..	X	X	X	X							
arcticus	..	X	X	X	X	X						
corniculum	..	..	X	..	X							
edwardsi	..	..	..	..	X							
cornutus	X	..	X									
vigilax	X	..	X	..	X	X						
atlanticus	X	..	X	..	X							
tenuiremis	..	..	..	..	X							
grandis	..	..	X	..	X							
crassus	..	..	X	..	X							
robustus	..	X	X	X	X							

[2] The records of surface catches of adults of *S. atlanticus*, *S. cornutus* and *S. vigilax* have been taken from the reports of other expeditions.

[3] The catches of *S. mollis* at 600, 800 and 1,000 meters were all made at Station 2894. The lower transparency of the water in this region as compared with the Sargasso Sea, where most of the other hauls were made, may account, in part, for this occurrence of *S. mollis* at depths so much shallower than those at which it is usually taken.

species may be encountered in the area explored by "Atlantis." The records for *S. arcticus* were made at Stations 2463 and 2894, and for *S. mollis* at Stations 2475, 2666, 2667 and 2894; the other "Atlantis" specimens were all taken at Station 2667. Since most of the tows at Station 2667, from which most of the material was obtained, were made only at 400 and 800 meters, very little is known of the lower limits of any of these species. It is hoped that work on "Atlantis" in the near future at Station 2667 in greater depths will make the picture more nearly complete.

EXTERNAL FEATURES OF THE EYES

The accompanying figures (2–9) and Table II illustrate the amount of variation in the eyes of *Sergestes*. Since the body is less compressed and the bases of the antennal scales are broader in these forms than in

the acanthephyrids, the eyes are borne on relatively longer stalks to enable the animal to see in all directions when the eyes are extended laterally. Since the length of the carapace is apparently not a constant fraction of the total body length and since such robust species as *S. crassus* have a much shorter carapace in proportion to body size than slender species like *S. corniculum,* it was found that the ratio of the diameter of the cornea to the carapace length showed less clearly the actual comparative sizes of the eyes than did the ratio of the diameter of the cornea to the entire length of the cornea and eyestalk and the

TABLE II

Relative size of the cornea as compared with the length of the carapace and the combined length of eyestalk and cornea in thirteen species of *Sergestes.*

Species	Ratio Diameter of cornea to Length of cornea plus eyestalk	Ratio Length of cornea to Length of cornea plus eyestalk	Ratio Diameter of cornea to Length of carapace
Sergestes			
mollis	0.34	0.25	0.052
sargassi	0.40	0.31	0.085
pectinatus	0.45	0.36	0.099
arcticus	0.46	0.38	0.090
corniculum	0.47	0.43	0.072
edwardsi	0.54	0.37	0.098
cornutus	0.56	0.34	0.092
vigilax	0.57	0.44	0.097
atlanticus	0.58	0.42	0.105
tenuiremis*	0.63	0.53	0.088
grandis*	0.63	0.57	0.081
crassus*	0.65	0.50	0.132
robustus*	0.67	0.67	0.115

* Luminescent species.

portion of the entire cornea and stalk occupied by the cornea. Even the latter comparisons are far from ideal as some species such as *S. arcticus* apparently have a longer stalk than others, but a more trustworthy comparison could not be found. Every part of a prawn which might be compared to the diameter of the eye is found to show some specific variation.

It is apparent from the accompanying figures that by far the smallest eyes in proportion to body size are to be found in *S. mollis* (Fig. 2), the only Atlantic species that obviously is restricted, for the most part, below the 1,000 meter zone. This species is a soft-bodied form, red in color, and it recalls to mind *Hymenodora* among the acanthephyrids,

although the eyes are far less degenerate than in the latter. One other sergestid, *Petalidium obesum,* very probably inhabits a similar depth and the eyes in it are possibly even smaller than in *S. mollis.* The form

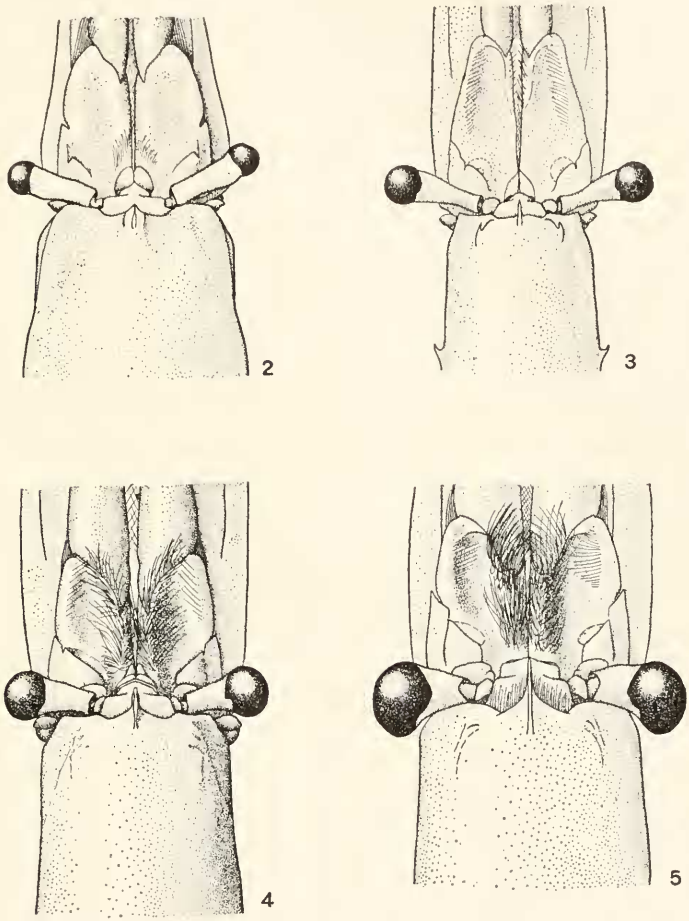


FIG. 2. *Sergestes mollis* Smith, male, 48 mm. in length. A species which is usually taken below the photic zone. Photophores absent. × 5.

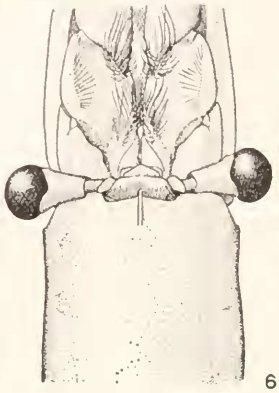
FIG. 3. *Sergestes arcticus* Kröyer, male, 40 mm. in length. Photophores absent. × 5.

FIG. 4. *Sergestes grandis* Sund, female, 56 mm. in length. Photophores present. × 5.

FIG. 5. *Sergestes robustus* Smith, male, 58 mm. in length. Photophores present. × 5.

with the largest eyes, *S. robustus* (Fig. 5) is not, as might be expected, one of the species that frequents the surface layers. In fact, those four species which have the broadest eyes in proportion to the stalk, *S.*

tenuiremis (Fig. 6), *S. grandis* (Fig. 4), *S. crassus* (Fig. 8), and *S. robustus*, are seldom taken in the upper 400 meters. Next in order above these (possibly by chance) are the three species which have been



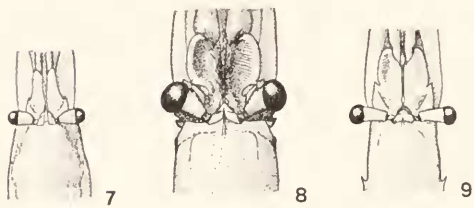


FIG. 6. *Sergestes tenuiremis* Kröyer, male, 52 mm. in length. Photophores present. × 5.

FIG. 7. *Sergestes cornutus* Kröyer, female, 14 mm. in length. Photophores absent. × 5.

FIG. 8. *Sergestes crassus* Hansen, male, 24 mm. in length. Photophores present. × 5.

FIG. 9. *Sergestes atlanticus* H. Milne Edwards, female, 18 mm. in length. Photophores absent. × 5.

found at the surface, and between this group and *S. mollis* are five species with rather small eyes which, so far as is known, frequent the lower part of the photic zone.[4]

[4] The investigations of Welsh, Chace and Nunnemacher (1937), and more recent unpublished studies, indicate that certain of the sergestids undergo extensive diurnal vertical migrations. The level of maximum numbers of a given species may be between the surface and 200 meters during the night and between 600 and 800 meters during the day. Therefore it is impossible to state that a certain species lives normally at a certain depth, and the most one can say is that the majority of the sergestids live in the photic zone and perhaps only one species in the North Atlantic, *S. mollis*, normally occurs below the level to which light penetrates.

If these figures present a true picture of the relative sizes of the eyes in the various species examined, one would naturally look for some factor to account for the large eyes of the four species at the bottom of the table. We believe that the answer may be found in the possibility that those species possess luminescent organs or photophores.

Until the sergestids of the "Michael Sars" expedition were reported upon by Sund in 1920 there was but one North Atlantic species, *S. splendens* Hansen, which was known to have photophores. Sund mentioned some pigmented spots in three other species, *S. grandis, S. crassus* (=*S. splendens* Sund), and *S. robustus,* which he suggested might be luminous organs. From the material of these three species collected by "Atlantis" we have been able to confirm his observations, and, although no histological preparations have as yet been made of this material, the position of the spots parallels so closely that of the photophores in those species which unquestionably possess them that there seems little doubt that such is their function. *S. crassus* and *S. robustus* apparently have these spots only on the antennal scales and outer uropods, while *S. grandis* (Fig. 1) has them scattered about the body and legs, particularly under the thorax and abdomen. In one large specimen of the latter species no less than 167 of these structures were counted. Hansen (1922) apparently doubted that these spots were actually photophores since they were not equipped with the lens-like structure found in the photophores of most other decapods and so become invisible in specimens preserved in alcohol or for too long in formalin. However, Kemp (1925) has described what he believes to be luminous organs in three species of pandalids from the Indian Ocean and these differ in structure from those which are known of other decapods in lacking any external trace of a lens.

If, then, the assumption is allowed that these structures are luminescent, only *S. tenuiremis* remains of those species which have the ratio of cornea to length of eyestalk greater than 0.60 and the ratio of the length of the cornea to the eyestalk greater than 0.50. Because no luminiscent structures were known in that species, a careful examination of a large male specimen was made. Although the specimen had been in formalin for about seven months and the characteristic red color had consequently disappeared, a pair of large, whitish organs were found in the coxae of the last pair of thoracic legs near the openings of the vasa deferentia. Sections made from one of these organs proved that they were almost certainly a cluster of at least three large photophores with well developed lenses entirely enveloped by the surrounding tissues. Their position and the absence of an external lens

closely parallels the structures described by Kemp in the Indian pandalids.

The evidence presented would indicate that there is some correlation between the size of the cornea in the species of *Sergestes* which live near the limit of light penetration and the presence or absence of luminescent organs. In the other five species which are known to have photophores, *S. challengeri* Hansen, *S. fulgens* Hansen, *S. prehensilis* Bate and *S. splendens* Hansen the eyes are described and figured as large, although the figures are usually not sufficiently accurate to permit actual measurements. O. Pesta (1918) described structures on the inner side of the carapace in *S. corniculum* which he suggested might be photophores, but if these spots do prove to be luminous the proposed theory obviously does not hold for this species.[5]

Approximately one half of the described North Atlantic species possess a small tubercle on the inner margin of the eyestalk near the cornea. It may be of interest to list here the species which have or do not have this tubercle, although there seems to be no correlation between the presence or absence of such a structure and the presence or absence of photophores or the size of the cornea.

Tubercle present	Tubercle absent
S. armatus	*S. arcticus*
S. corniculum	*S. atlanticus*
S. crassus	*S. cornutus*
S. grandis	*S. edwardsi*
S. pectinatus	*S. mollis*
S. sargassi	*S. robustus*
S. tenuiremis	*S. splendens*
	S. vigilax

[5] According to Burkenroad (1937) Organs of Pesta are probably present in all species of sergestids excepting *S. mollis, S. tenuiremis* and *S. challengeri.*

Figures 10–15 inclusive are all from dorso-ventral sections of eyes, unstained, × 32.

Fig. 10. Photomicrograph of a section of an eye of *Sergestes corniculum* made by means of transmitted light.

Fig. 11. The same preparation as in Fig. 10 photographed by means of dark-field illumination. The reflecting pigment which is more abundant in the dorsal part of the eye may be readily distinguished from the screening pigment.

Fig. 12. Photomicrograph of a section of an eye of *Sergestes robustus* made by means of transmitted light.

Fig. 13. The same preparation as in Fig. 12 photographed by means of dark-field illumination. The reflecting pigment is more abundant in the dorsal region which is toward the left.

Fig. 14. Photomicrograph of a section of an eye of *Sergestes mollis* made by means of transmitted light.

Fig. 15. The same preparation as in Fig. 14 photographed by means of dark-field illumination. The reflecting pigment is more evenly distributed throughout the region of the eye where it normally occurs.

FIGS. 10–15

Structure and Pigmentation of the Eyes

The eyes of eight species of sergestids were sectioned and examined histologically. The structure of these eyes was found to be essentially like that of deep and shallow-water shrimps and prawns whose eyes have been frequently described. One feature common to all was found to be the large and clearly defined rhabdomes, the receptor elements of the eye. The most striking differences were seen in the amounts and distribution of screening and reflecting pigments.

The eyes of *S. grandis* and *S. temuicrnis* resemble those of *S. robustus* (Figs. 12 and 13). It has already been pointed out that these three species possess photophores and this probably accounts for their large eyes. This may also be the reason for the large amount of reflecting pigment found in these eyes. Its distribution is such that the periphery of the eye may be more sensitive to differences in light intensity than the central portion, and the larger amount of proximal pigment in the central portion of the eye may conceivably increase the visual acuity of the region by a partial isolation of the rhabdomes from one another.

S. corniculum (Figs. 10 and 11), *S. arcticus, S. armatus* and *Petalidium obesum* probably do not possess photophores and certain of them may inhabit a region of higher light intensity than the three mentioned above. Of these forms only the first has any reflecting pigment in the eye, the others completely lacking this set of pigment. *S. arcticus* and *P. obesum* have a large amount of black, proximal, screening pigment.

Since *S. mollis* normally lives below the photic zone, as does the acanthephyrid *Hymenodora glacialis*, one might expect to find that its eyes were equally degenerate but such is not the case. They are the smallest, in relation to body size, of all the sergestids examined by us, but structurally the eye shows very little modification which may be correlated with life in a zone to which sunlight does not penetrate (Figs. 14 and 15). The even distribution of reflecting pigment may conceivably be related to the conditions under which the animal lives, but there are fairly large amounts of distal and proximal screening pigments. In *Hymenodora* (Welsh and Chace, 1937) it was shown that screening pigments were completely lacking, the rhabdomes had disappeared and there was an abnormally large amount of reflecting pigment. Hence the eye was considered to be quite degenerate and capable of doing no more than registering changes in light intensity.

Decapod crustaceans which are known with certainty to dwell exclusively in the vast intermediate region of the sea, between the lower limit of the photic zone and the bottom (excepting the bottom fauna),

are not numerous as regards species. Until more have been studied it will be impossible to determine the exact trend in the degeneration of the eye as a result of living in complete darkness. From the work thus far carried out, however, it appears that depth, hence light intensity, modifies the eye, but in addition the possession of photophores and the ability to produce light is a most important factor in this adaptation.

Summary

1. Fourteen species of *Sergestes* have been taken in closing nets from the western part of the North Atlantic and the size and structure of their eyes have been related to the depth at which certain species occur and to the presence or absence of photophores.

2. *Sergestes mollis* is ordinarily taken below the photic zone and this species lacks photophores. The corneal portion of the eye of this form is smaller in relation to body size than is that of any other species studied. The eyes, however, are not so degenerate structurally as those of *Hymenodora glacialis,* an acanthephyrid having a similar vertical distribution.

3. *Sergestes tenuiremis, S. grandis, S. crassus and S. robustus* have been shown to possess organs which are probably photophores and these four species have the largest eyes in respect to body size of all which have been studied. Hence it may be concluded that the production of light by such an organism influences in some way the development of the eye. This agrees with the findings on the acanthephyrids.

4. The remainder of the sergestids studied which live within the photic zone have eyes smaller than those which possess photophores and in certain cases (*S. arcticus* and *S. armatus*) the pigmentation of the eye is quite unusual.

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